Mobility of Mass-Reared Diapaused and Nondiapaused *Cydia pomonella* (Lepidoptera: Tortricidae): Effect of Mating Status and Treatment with Gamma Radiation

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ABSTRACT Mass-reared insects may differ in their behavioral traits depending on whether they have undergone diapause. We studied the mobility of mass-reared diapaused and nondiapaused *Cydia pomonella* (L.) with a focus on understanding the effect of mating status and treatment with gamma radiation as these insects are destined for use in an areawide program that uses the sterile insect technique (SIT). Actograph-measured mobility was assessed one gender at a time for 4 h during which the photoperiod transitioned from day to night. We tested 20–30 individuals per treatment. For experiments on the effect of mating status, we used 24–48-h-old adults (diapause [D]-virgin, D-mated, standard [N]-virgin, and N-mated), which is the typical age class that is released in the SIT program. Diapaused females were significantly more mobile than females reared through standard production, whereas no differences were detected in male mobility because of rearing strategy. Mated females were significantly more mobile than virgin females, whereas no difference in mobility because of mating status was detected for males. Mated females were significantly more mobile than mated males. In contrast, virgin females were significantly less mobile than virgin males. For experiments on the effect of treatment with gamma radiation, adults from all rearing strategies and treatments (D-0Gy, D-100Gy, D-250Gy, N-0Gy, N-100Gy, and N-250Gy), were tested simultaneously. Adult males were tested at two different constant temperatures (25 and 20°C), whereas adult females were tested only at 25°C. For standard-reared adults, we found a significant linear decrease in mobility as the radiation dose increased from 0 to 250 Gy. In contrast, the relationship between mobility and dose of radiation was quadratic for diapaused males and absent for diapaused females.

KEY WORDS codling moth, sterile insect technique, quality control, diapause, mobility

Diapause is a syndrome of developmental, physiological, biochemical, and behavioral attributes that together serve to enhance insect survival during seasons of environmental adversity (Denlinger 2003). In codling moth, *Cydia pomonella* (L.), diapause is facultative and is expressed during the last larval instar (Brown 1991). In the field, the overwintered (diapaused) generation emerges in the spring and is followed by one or more summer generations depending on the insect's geographical location (Shel'Deshova 1962). In the laboratory, codling moth larvae may be induced into diapause by exposure to short day photoperiods and low temperatures that usually predict the onset of winter (Singh and Ashby 1986). Techniques to mass-rear codling moth through diapause were published by Bloem et al. (1997, 2000).

Codling moth mobility has been shown to be a heritable trait (Schumacher et al. 1997b, Keil et al. 2001b) highlighting the possible importance of endogenous factors on the locomotor activity for this and other lepidopteran species. Recently, Vallat and Dorn (2005) found that volatiles emitted from apple trees in early spring were repellent to female codling moths and suggested that such repellency might facilitate emigration of a proportion of the population to colonize new habitats. Hence, in this instance, diapaused females might benefit from having higher mobility. Field dispersal of mass-reared and gamma-irradiated diapaused and nondiapaused codling moths was studied by Bloem et al. (1998). These authors found that the proportion of recaptured diapaused moths was significantly higher than the proportion of recaptured nondiapaused moths regardless of whether dispersal was measured using nondirected techniques (passive interception traps) that recapture both genders or directed techniques (natural or synthetic pheromone-

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baited traps) that capture only males. Nevertheless, laboratory experiments that directly compare the mobility of adult males and females reared through diapause or through standard (nondiapause) protocols have not been conducted.

Sublethal doses of certain products used in moth control have been shown to modify insect behavior. For example, the neurotoxin azinphosmethyl increased locomotor activity in male and female codling moth (Dorn and Gu 1999) and accelerated egg deposition in female codling moth (Abivardi et al. 1998). In addition, the juvenile hormone mimic fenoxycarb modified the diel pattern of activity in female codling moth (Keil et al. 2001a), whereas the ecdysone mimic methoxyfenozide negatively affected the ability of leafroller males to respond to calling females (Hoelscher and Barrett 2003).

The Okanagan-Kootenay Sterile Insect Release (OKSIR) Program in Osoyoos, British Columbia, Canada, seeks long-term and sustainable areawide control of codling moth through the release of mass-reared and irradiated insects of both genders (Bloem and Bloem 2000). Since 1994, when the first moth releases were made (Dyck et al. 1993), the OKSIR Program has significantly reduced feral codling moth populations as well as the use of organophosphate sprays in the initial ≈3,000-ha treatment area (Bloem et al. 2006a). Nevertheless, the long-term sustainability of the program (Dendy et al. 2001) as well as the quality of the insects used to effect areawide control continues to be debated. Release–recapture experiments conducted in an effort to evaluate and improve the quality of the mass-reared moths indicated that field performance of male codling moths reared through diapause was significantly higher than that of males reared through standard production, even when treated with the same high dose of gamma radiation (330 Gy) (Bloem et al. 1998). The encouraging results on inherited sterility and its positive effect on codling moth field performance (Bloem et al. 1999a,b, 2001) prompted additional research that compared the field quality of diapaused and nondiapaused male codling moth treated with substerilizing doses of gamma radiation (150 and 250 Gy) (Bloem et al. 2004). Again, field performance of released males was significantly improved by rearing through diapause and by lowering the dose of radiation used to treat the insects. These effects were observed in spring when field temperatures were cool and in summer when evening temperatures were high, independent of the sampling method used for evaluation (i.e., capture in pheromone-baited traps, virgin female-baited traps, or in mating tables). Interestingly, the reduction in field performance because of dose of radiation was greater when males had been mass-reared through standard (nondiapause) production, suggesting that rearing through diapause might attenuate some of the negative effects of treatment with gamma radiation (Bloem et al. 2004). Nevertheless, more information is needed to further explain how adult dispersal (either directed or nondirected) might be influenced by endogenous factors (adult mating status and rearing strategy) and by treatment with gamma radiation for male and female codling moth.

In *C. pomonella*, computer-linked actographs have been used to document daily patterns of locomotor activity for different genders (Knight et al. 1994, Keil et al. 2001a), to select strains with high and low mobility that were confirmed as such in field dispersal studies (Keil et al. 2001b) and to examine sublethal effects of different management techniques on the mobility of adult moths (Dorn et al. 1999, Dorn and Gu 1999, Keil et al. 2001a). In the current study, we compared the locomotor activity of virgin or mated diapaused and nondiapaused codling moth, and we documented the effect of increasing doses of gamma radiation on this behavioral trait. In a companion article (Bloem et al. 2006b), we examine the effect of constant temperature and length of adult moth cold storage on the mobility of similarly reared moths. Our results are presented herein and their ecological significance and importance to the implementation of a successful areawide SIT program for codling moth are discussed.

Materials and Methods

Test Insects. The codling moth colony used in these experiments has been in continuous culture at the OKSIR mass-rearing facility in Canada since 1993 (≈10 generations/yr). Routine introductions of feral males (replacing 50–100% of laboratory males) are made in the winter of most years. Larvae are reared on a modified agar-free artificial diet originally developed by Brinton et al. (1969). Insects were reared through two different strategies. For standard (N) production, codling moth eggs were placed on trays of diet and reared at constant temperature (27°C) and a photoperiod of 16:8 (L:D) h. Relative humidity (RH) was 55% at egg eclosion and was lowered to 30% by the time pupation occurred. At day 24, trays of diet were chosen at random and destructively sampled to obtain pupae of roughly the same age. Pupae destined for the study on the effect of mating status were sorted by gender, placed in plastic petri dishes, and kept at 27°C, 70% RH, a photoperiod of 16:8 (L:D) h, until shipment to Switzerland. Pupae destined for the study on the effect of treatment with gamma radiation were sorted by gender and placed in separate aluminum screen cages (30 by 30 by 30 cm) at 27°C, 70% RH, and a photoperiod of 16:8 (L:D) h to allow for adult emergence. Adults were collected three to four times per day and stored in plastic petri dishes (9 cm in diameter) at 0–2°C until irradiation and shipment to Switzerland.

Diapause (D) was induced in neonate larvae on 11 August 2004 by shortening the photoperiod and lowering the temperature (12L-25°C:12D-21°C) during rearing; relative humidity followed the same pattern as described above. Diapaused larvae were collected into corrugated cardboard rolls placed on top of the diet from day 23 to 37, conditioned (at 15°C and 0:24 [L:D] h from 17 September until 23 December 2004), and stored (at 0–2°C and 0:24 [L:D] h for a minimum of

100 d) as outlined in Bloem et al. (1997, 2000). Diapause was terminated by placing the larvae at 27°C and a photoperiod of 16:8 (L:D) h. After 9 d, pupae of similar age were collected by destructively sampling each roll. As described above, pupae destined for the study on the effect of mating status were sorted by gender, placed in plastic petri dishes, and kept at 27°C, 70% RH, and a photoperiod of 16:8 (L:D) h until shipment to Switzerland. Pupae destined for the study on the effect of treatment with gamma radiation were sorted by gender and placed in separate screen cages to allow for adult emergence. Adults were collected three to four times per day and stored in petri dishes at 0–2°C until irradiation and transport to Switzerland.

Effect of Mating Status on Locomotor Activity. Pupae were shipped via courier to the Institute of Plant Sciences/Applied Entomology, Swiss Federal Institute of Technology (ETH), Zurich, Switzerland, in petri dishes inside a small insulated box with ice packs. An electronic data pod (Hobo, Onset, Bourne, MA) was included to record temperature during transport. Upon arrival, pupae of each rearing strategy (D and N) and gender (M and F) were placed in separate plastic emergence cages (21 by 21 by 17 cm) and kept at 26°C, 65% RH, and a photoperiod of 16:8 (L:D) h. Emerging adults were collected once per day and placed individually in glass vials (28 by 80 mm) and given access to moisture. Fifty percent of the adults were paired with a virgin adult of the opposite gender. All insects (virgins and pairs) were kept at 26°C, 65% RH, and a photoperiod of 16:8 (L:D) h for 24 h.

We conducted preliminary actograph studies using adults of different age classes. Because no significant difference was found in the mobility of males aged 2, 3, 4, and 5 d for all treatments described below (unpublished data), we chose to use only the age class that best represents the insects that are typically released by the OKSIR Program (those that are between 24 and 48 h old). The locomotor activity of virgin and mated adults from each rearing strategy (N-virgin, N-mated, D-virgin, and D-mated) was tested one gender at a time. Mating status for males was confirmed before testing by dissecting the female to verify the presence of a spermatophore in the bursa copulatrix (Ferro and Akre 1975). Mated females were dissected after testing to confirm their mating status.

Experiments were conducted using 30 infrared actographs (Activity Monitor, Electronic Services Unit, University of New England, Armidale, New South Wales, Australia) located inside a walk-in climate controlled chamber (Conviron, model PGV 36, Controlled Environments Limited, Winnipeg, Manitoba, Canada). Each actograph consists of a transmitter that emits an infrared light beam that is captured by a receiver/logic-converter linked to a computer. Test insects in closed glass vials are positioned between the transmitter and the receiver. Any movement that intercepts the infrared beam triggers a signal that is recorded by the computer.

Tests lasted 4 h, and two 4-h testing periods were used each day (1200–1600 and 1800–2200 hours). To minimize variation, all cohorts assayed on the same day were transferred to a chamber maintained at 25°C and a photoperiod of 24:0 (L:D) h 4 to 8 h before testing. Vials with adults were placed in the actographs at random, and experiments always were initiated 1 h before the onset of dusk. Light intensity was 3,750 lux at photophase (1 h) and 0.1 lux at scotophase (1 h). Between these two phases, there was a simulated dusk period lasting 2 h, during which illumination was gradually decreased from 3,750–0.1 lux in 10-min steps. Temperature and relative humidity remained constant and were 25°C and 60%, respectively. In total, 25–30 individuals of each rearing strategy, mating status and gender were tested over 4 d.

Effect of Gamma Radiation on Locomotor Activity. Approximately 100 newly emerged (0–24-h-old) adults of each rearing strategy and gender (N male, N female, D male, and D female) were either left untreated (0 Gy) or were treated with two substerilizing doses of gamma radiation (100 or 250 Gy) using a $Cobalt^{60}$ source (Gammacell 220, Nordion, Canada; dose rate of 6.77 kGy/h). After treatment, adults were packaged in petri dishes in a small insulated box with ice packs. As described above, an electronic data pod was included to record temperatures during transport. Moths traveled via commercial airline to Zurich, Switzerland (approximate time in transit, 22 h). Upon arrival, adults of each treatment were placed individually in glass vials (28 by 80 mm) with access to moisture and stored at 2°C and a photoperiod of 0:24 (L:D) h until tested.

Experiments were conducted using the equipment described above. Cohorts of virgin adults from each treatment (N-0Gy, N-100Gy, N-250Gy, D-0Gy, D-100Gy, and D-250Gy) were tested simultaneously one gender at a time for a period of 4 h. Three 4-h testing periods were used per day (1000–1400, 1600–2000, and 2200–0200 hours), and all evaluations were completed within 6 d of shipment arrival. Insects were allowed to acclimate at 25°C (or 20°C) and a photoperiod of 24:0 (L:D) h for 2 h before testing. Vials with codling moth individuals were placed in the actographs at random and all tests were initiated 1 h before the onset of simulated dusk. Light varied between 3,750 lux at photophase (1 h) and 0.1 lux at scotophase (1 h). In total, 20–30 individuals of each rearing strategy and gender (N male, N female, D male, and D female) were tested at each radiation dose (0, 100, and 250 Gy). Males were tested at two different constant temperatures (25 and 20°C), whereas females were tested only at 25°C. Relative humidity inside the chamber was maintained at 60% for the duration of the experiments.

Data Analysis. In the actographs, any movement that intercepts the infrared beam triggers a signal that is recorded by the computer as a mobility count. *C. pomonella* adults intercepted the infrared beam nearly exclusively by flight (S.B., unpublished data). Because artificially elevated counts can occur when an insect flutters in the path of the infrared beam, recorded signals that occurred more than twice within the same second of time were eliminated by application of a specific analytical program (M. Gernss,

ETH). Thus, a mobility count is defined as an interception of the infrared beam excluding this artifact.

Effect of Mating Status on Locomotor Activity. Mobility counts per individual were summed and analyzed using multifactor analysis of variance (ANOVA) with gender (male [M] or female [F]), rearing strategy (D or N), mating status (virgin [V] or mated [M]), test time (1200–1600 and 1800–2200 hours), and test day as sources of variation (PROC GLM, SAS Institute 1989). All interactions were included in the statistical model. When significant differences were indicated, means were separated by the Tukey–Kramer statistic at $P = 0.05$ (SAS Institute 1989).

Effect of Dose of Gamma Radiation on Locomotor Activity. Mobility counts for individual males were summed, $\log_{10}$ transformed to stabilize their variance, and analyzed using multifactor ANOVA with rearing strategy (D or N), dose of radiation (0, 100, and 250 Gy), test time (1000–1400, 1600–2000 h, and 2200–0200 hours), and test temperature (20 or 25°C) as sources of variation (PROC GLM, SAS Institute 1989). All interactions were included in the statistical model. When significant ($P \leq 0.05$) interactions were detected between rearing strategy and treatment dose, and between overall temperature and treatment dose, the effects were examined using polynomial regression (SAS Institute 1989).

Mobility counts per individual female were summed, $\log_{10}$ transformed to stabilize the variance, and analyzed using multifactor ANOVA with rearing strategy (D or N), dose of radiation (0, 100, 250 Gy), and test time (1000–1400, 1600–2000, and 2200–0200 hours) as sources of variation (PROC GLM, SAS Institute 1989). All interactions were included in the statistical model. When a significant ($P \leq 0.05$) interaction was detected between rearing strategy and treatment dose, the effect because of dose was examined using polynomial regression (SAS Institute 1989).

Results

Effect of Mating Status on Locomotor Activity. Statistical analysis revealed a significant interaction between codling moth gender and rearing strategy ($F = 6.28$; df = 1, 179; $P = 0.0131$) (Fig. 1). Diapaused females were significantly more mobile than females reared through standard (nondiapaused) production. However, there was no significant difference in the mobility of males reared through standard production or through diapause. In addition, we found no significant difference in the mobility of adult males and females within each rearing strategy.

The locomotor activity of adult codling moths was also significantly influenced by an interaction between insect gender and mating status ($F = 18.68$; df = 1, 179; $P < 0.0001$) (Fig. 2). Mated females were significantly more mobile than virgin females. However, no difference in mobility due to mating status was detected for males. We also found significant differences between the mobility of mated males and mated females and between virgin males and virgin females. Mated females were significantly more mobile than mated males. In contrast, virgin females were significantly less mobile than virgin males.

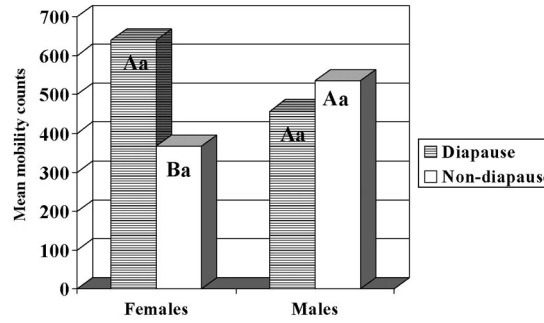

Fig. 1. Effect of rearing strategy on the locomotor activity of 24–48-h-old female and male mass-reared *C. pomonella*. Uppercase letters denote significance within gender; lowercase letters denote significance within rearing strategy. Twenty to 30 individuals per treatment were tested.

Effect of Dose of Gamma Radiation on Locomotor Activity. The locomotor activity of adult male codling moths was significantly influenced by an interaction between rearing strategy and dose of radiation ($F = 3.28$; df = 2, 320; $P = 0.039$) (Fig. 3). When males were reared through standard (nondiapaused) production, there was a significant linear relationship between treatment dose and locomotor activity ($y = 1.387 - 0.0023x$, $P < 0.0001$, $r^2 = 0.1$). When males were reared through diapause, there was a significant quadratic relationship between locomotor activity and dose of radiation ($y = 1.24 + 0.0028x - 0.000027x^2$, $P = 0.0011$, $r^2 = 0.28$). For both types of males, locomotor activity was significantly reduced as the dose of radiation increased from 0 to 250 Gy.

Adult male mobility was significantly influenced by an interaction between dose of radiation and ambient temperature ($F = 4.06$; df = 2, 320; $P = 0.0181$) (Fig. 4). At 25°C, there was a significant quadratic relationship between locomotor activity and dose ($y = 1.45 + 0.0038x - 0.00003x^2$, $P = 0.0011$, $r^2 = 0.24$), whereas at 20°C the significant relationship between

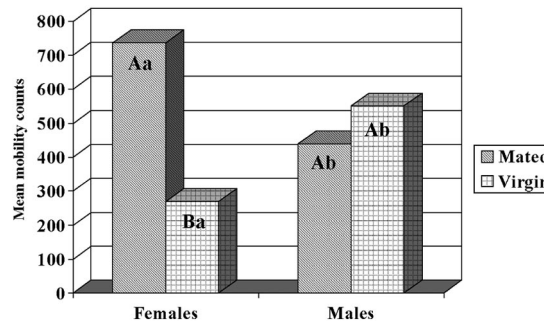

Fig. 2. Effect of mating status on the locomotor activity of 24–48-h-old female and male mass-reared *C. pomonella*. Uppercase letters denote significance within gender; lowercase letters denote significance within mating status. Twenty to 30 individuals per treatment were tested.

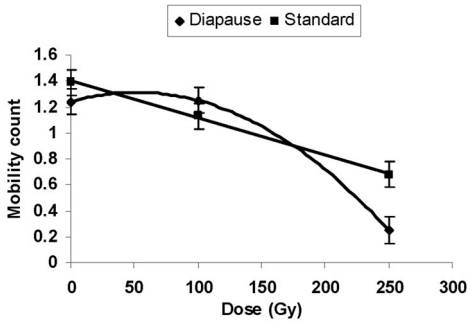

Fig. 3. Effect of dose of gamma radiation (0, 100, and 250 Gy) on the locomotor activity of adult male *C. pomonella* reared through diapause or standard (nondiapause) production. Mean mobility counts were $\log_{10}$ transformed to stabilize the variance. Equations describing the relationship between mobility and dose are as follows: for standard males $y = 1.387 - 0.0023x$, $P < 0.0001$, $n = 173$; for diapaused males $y = 1.24 + 0.0028x - 0.000027x^2$, $P = 0.0011$, $n = 173$.

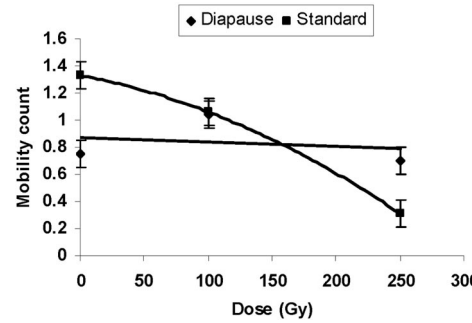

Fig. 5. Effect of dose of gamma radiation (0, 100, and 250 Gy) on the locomotor activity of adult female *C. pomonella* reared through diapause or standard (nondiapause) production. Mean mobility counts were $\log_{10}$ transformed to stabilize the variance. The equation describing the relationship between mobility and dose for standard females is $y = 1.33–0.0018x$, $P < 0.0001$, $n = 71$.

these parameters was linear ($y = 1.181 - 0.003x$, $P < 0.0001$, $r^2 = 0.15$). At both temperatures, male locomotor activity was significantly reduced as the dose of radiation increased from 0 to 250 Gy. Mobility counts for males treated with 100 Gy were significantly lower at an ambient temperature of 20 than of 25°C.

Female locomotor activity was significantly influenced by an interaction between rearing strategy and dose of radiation ($F = 4.91$; df = 2, 123; $P = 0.0088$) (Fig. 5). For females reared through standard (nondiapaused) production, there was a significant linear relationship between dose of radiation and mobility ($y = 1.33 - 0.0018x$, $P < 0.0001$, $r^2 = 0.27$). However, no linear relationship was observed between mobility and dose of radiation for female moths that had been reared through diapause. Locomotor activity was significantly reduced as the dose of radiation used to treat standard-reared females increased from 0 to 250Gy.

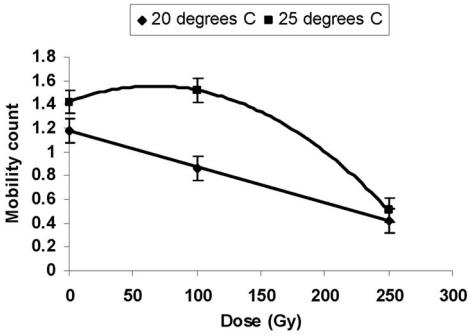

Fig. 4. Effect of test temperature (20 or 25°C) and dose of gamma radiation (0, 100, and 250 Gy) on the locomotor activity of adult male *C. pomonella*. Mean mobility counts were $\log_{10}$ transformed to stabilize the variance. Equations describing the relationships between mobility and dose are as follows: for tests conducted at 25°C $y = 1.49 + 0.0038x - 0.00003x^2$, $P = 0.0011$, $n = 173$; for tests conducted at 20°C $y = 1.181 - 0.003x$, $P < 0.0001$, $n = 173$.

The mobility of control females in the trial on effect of radiation (Fig. 5) was lower than the mobility of females used in the comparison of genders (Fig. 1). In the first case, adult females were shipped before testing and were at least 7–10 d old when tested on the actograph. In the second case, insects were shipped as pupae and tested as adults 24–48 h after adult emergence.

It should be noted that the mobility observed for diapaused females in Figs. 1 and 5 is different. This discrepancy may have resulted from a difference in insect age at the time of testing. Females in Fig. 1 were 24–48 h old, whereas females in Fig. 5 were at least 7–10 d in age when tested in the actograph. We hypothesize that fat reserve depletion is more critical to diapaused females, and, as such, older females are more affected by aging that nondiapaused females. Future studies should be conducted to investigate this relationship.

Discussion

Our objective when designing these experiments was to improve our basic understanding of how adult dispersal and pheromone trap-measured flight might be influenced by selected endogenous factors and treatment parameters that can be managed or modified when mass-rearing *C. pomonella* destined for sterile insect release. Our results showed that preimaginal life history through diapause significantly increased the actograph-measured mobility of adult females compared with that of females reared without diapause. This finding supports the hypothesis of Vallat and Dorn (2005) that early spring might be the period when a proportion of the population undertakes long flights in search of new habitats. Even though the habitat of this species consists of perennial fruit trees, the amount of food resources available at any one time is subjected to fluctuations because of biannual fruit bearing patterns (Keil et al. 2001b). In addition, the propensity for higher mobility and dispersal in female

moths may be an evolved adaptation to increase the chances that they will be able to locate and make use of scattered wild fruit-bearing trees within the original habitat (Schumacher et al. 1997a). Whether within the original habitat or even within an orchard setting, suitable oviposition sites on fruit-bearing trees in the spring represent a patchy resource in time and in space. As such, higher mobility and flight propensity may be an evolved adaptation for an overwintered (diapaused) female needing to locate and exploit these patchy resources.

Our data showed that mated females were significantly more mobile than virgin females irrespective of rearing strategy. Virgin female codling moths were observed to remain fairly stationary during several hours at the initiation of scotophase while involved in calling behavior (Castrovillo and Cardé 1979). Field oviposition by mated females was observed to occur primarily during sunset with females quickly moving away or taking flight immediately after ovipositing (Borden 1931). In addition, Schumacher et al. (1997a) showed that 2-d-old mated codling moth females had greater total distance flown and a higher number of flights than did virgin females of the same age when measured using the flight mill. Schumacher et al. (1997a) also showed that the peak flight capacity for mated females occurred 1 to 3 d after eclosion, which would correspond with their major egg-laying period. Our data agree with the field observations reported by Borden (1931) and with laboratory observations and assays published by Castrovillo and Cardé (1979) and Schumacher et al. (1997a).

Our experiments showed that the locomotor activity of male codling moths was significantly influenced by an interaction between rearing strategy and dose of radiation. The decrease in mobility for standard-reared (nondiapaused) males was linear as the treatment dose increased from 0 to 250 Gy. In contrast, the relationship between mobility and dose for diapaused males was quadratic, indicating that mobility in diapaused males was not reduced below that of untreated males (0 Gy) when the treatment dose was low. These data are congruent with the field results obtained by Bloem et al. (2004) and provide strong evidence to support the hypothesis that diapaused males are better able to tolerate the adverse effects of treatment with gamma radiation.

Not unexpectedly, male mobility was influenced by an interaction between treatment dose and test temperature. Irrespective of whether experiments were conducted at constant temperatures of 25 or 20°C, male locomotor activity was significantly reduced as the treatment dose increased from 0 to 250 Gy. Although Hsiao (1978) used actographs to examine the circadian activity of *Helicoverpa zea* (Lepidoptera: Noctuidae) at different constant temperatures, and several studies on diel patterns of activity using actographs have been published for codling moth (Knight et al. 1994, Dorn and Gu 1999, Keil et al. 2001a), the effect of gamma radiation on adult mobility at different temperatures has not been previously documented. These data provide unique insights into the effect of ambient temperature on irradiated codling moth mobility and further support the use of lower doses of gamma radiation when treated codling moths are released in the field, regardless of the seasonal temperature. Under field conditions, pheromone-mediated flight activity decreased significantly when the dose of radiation increased or when the temperature dropped below 16°C (Bloem et al. 2004). Because these data were collected using pheromone-baited traps, it was concluded that the decrease was not attributed to females that did not call but rather to males that did not respond to the synthetic pheromone signal. The results from our laboratory studies allow for the interpretation that this lacking response was most likely due to a reduced mobility in these males.

Female locomotor activity also was significantly influenced by an interaction between rearing strategy and dose of radiation. It is interesting to note that mobility in standard-reared (nondiapaused) females was significantly reduced as the dose of radiation increased (from 0 to 250 Gy) but there was no relationship between mobility and dose for diapaused (D) females. Indeed, the mobility of diapaused females irradiated with doses up to 250 Gy was not reduced at all. These data provide additional evidence to support the hypothesis that codling moth reared through diapause are better able to tolerate the adverse effects of treatment with gamma radiation. To our knowledge, this is the first study to demonstrate these effects in females. These data allow us to begin to understand the factors affecting the performance of irradiated and released females which constitute 50% of insects released during the application of the SIT for this species. As suggested by our results, the level of locomotor activity can be maintained in females by either treating them with lower doses of radiation or by rearing through diapause. Further studies are needed to fully understand the role of females and their calling activity on the effectiveness of the SIT for codling moth and other lepidopteran species.

Last, some methodological and procedural differences between the field studies conducted by Bloem et al. (1998, 2004) and the present laboratory experiments might explain some of the quantitative differences observed between the field and the laboratory data. We conclude that codling moth males reared through standard or through diapause production protocols exhibit similar generalized spontaneous mobility and dispersal capacity when subjected to the same treatments. However, diapaused mass-reared males that are treated with low doses of gamma radiation and released have an advantage over standard-reared and irradiated males in responding to stimuli that results in superior behavior-mediated (directed) flight. Because the quality of mass-reared insects is of primary importance to SIT programs (Böller and Chambers 1977), it is imperative to continually assess the ability of mass-reared insects to find and mate with wild females (or with wild males) under field conditions—the definition of insect quality given by Miyatake and Yamagishi (1993).

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